

CANADIAN JOURNAL OF RESEARCH

VOLUME 26

AUGUST, 1948

NUMBER 4

— SECTION D —

ZOOLOGICAL SCIENCES

Contents

	Page
On a <i>Physaloptera</i> Larva from an Insect— <i>M. A. Basir</i> - -	197
<i>Cameronia biovata</i> gen. et sp. nov. (Thelastomatidae), a New Nematode Parasite of the Mole Cricket, <i>Gryllotalpa</i> <i>africana</i> Beauv.— <i>M. A. Basir</i> - - - - -	201
Parasites of Freshwater Fish. IV. Internal Helminths Para- sitic in Speckled Trout (<i>Salvelinus fontinalis</i> (Mitchill)) in Rivers and Lakes of the Laurentide Park, Quebec, Canada— <i>L. P. E. Choquette</i> - - - - -	204
The Function of the Giant Axon of <i>Mysicola infundibulum</i> Montagu— <i>J. A. Colin Nicol</i> - - - - -	212

NATIONAL RESEARCH COUNCIL
OTTAWA, CANADA

CANADIAN JOURNAL OF RESEARCH

The *Canadian Journal of Research* is issued in six sections, as follows:

- | | |
|-----------------------|------------------------|
| A. Physical Sciences | D. Zoological Sciences |
| B. Chemical Sciences | E. Medical Sciences |
| C. Botanical Sciences | F. Technology |

For the present, Sections A, C, D, and E are to be issued six times annually, and Sections B and F, twelve times annually, each section under separate cover, with separate pagination.

The *Canadian Journal of Research* is published by the National Research Council of Canada under authority of the Chairman of the Committee of the Privy Council on Scientific and Industrial Research. The *Canadian Journal of Research* is edited by a joint Editorial Board consisting of members of the National Research Council of Canada, the Royal Society of Canada, and the Chemical Institute of Canada.

Sections B and F of the *Canadian Journal of Research* have been chosen by the Chemical Institute of Canada as its medium of publication for scientific papers.

EDITORIAL BOARD

<i>Representing</i>	<i>Representing</i>	
NATIONAL RESEARCH COUNCIL	ROYAL SOCIETY OF CANADA	
DR. A. R. GORDON, (<i>Chairman</i>), Head, Department of Chemistry, University of Toronto, Toronto.	DR. A. NORMAN SHAW, Chairman, Department of Physics McGill University, Montreal.	} Section III
DR. C. H. BEST, The Banting and Best Department of Medical Research, University of Toronto, Toronto.	DR. J. W. T. SPINKS, Department of Chemistry, University of Saskatchewan, Saskatoon.	
DR. ROBERT NEWTON, President, University of Alberta, Edmonton.	DR. E. HORNE CRAIGIE, Department of Zoology, University of Toronto, Toronto.	} Section V
DR. G. H. HENDERSON, Professor of Mathematical Physics, Dalhousie University, Halifax.	DR. H. S. JACKSON, Head, Department of Botany, University of Toronto, Toronto.	
<i>Ex officio</i>	<i>Representing</i>	
	THE CHEMICAL INSTITUTE OF CANADA	
DR. LÉO MARION, Editor-in-Chief, Division of Chemistry, National Research Laboratories, Ottawa.	DR. R. V. V. NICHOLLS, Associate Professor of Chemistry, McGill University, Montreal.	
DR. H. H. SAUNDERSON, Director, Division of Information Services, National Research Laboratories, Ottawa.		

EDITORIAL COMMITTEE

Editor-in-Chief,	DR. LÉO MARION	Editor, Section D,	DR. E. HORNE CRAIGIE
Editor, Section A,	DR. A. NORMAN SHAW	Editor, Section E,	DR. J. B. COLLIP
Editor, Section B,	{ DR. J. W. T. SPINKS	Editor, Section F,	{ DR. J. A. ANDERSON
	{ DR. R. V. V. NICHOLLS		{ DR. R. V. V. NICHOLLS
Editor, Section C	DR. H. S. JACKSON		{ DR. A. NORMAN SHAW

Manuscripts should be addressed:

*Editor-in-Chief,
Canadian Journal of Research,
National Research Council, Ottawa, Canada.*

Canadian Journal of Research

Issued by THE NATIONAL RESEARCH COUNCIL OF CANADA

VOL. 26, SEC. D.

AUGUST, 1948

NUMBER 4

ON A *PHYSALOPTERA* LARVA FROM AN INSECT¹

By M. A. BASIR²

Abstract

A *Physaloptera* larva is described from the body cavity of the earwig, *Labidura reparia* (Pallas).

About 50 earwigs were examined for nematode infection. No adult nematodes were obtained but two small larval specimens were found free and unencysted in the body cavity of one of them. These belong to the genus *Physaloptera* and are described below. Both the specimens are of approximately the same size.

Physaloptera sp.

(Larva)	1.43	?	48.8	J	94.29	2.1 mm.
	4.05	?	6.48	5.94	3.33	

The body length is 2.1 mm. The cuticle is striated only in the anterior one-fifth of the body, up to a distance of about 400μ from the anterior end, where striation suddenly ends. The larva is broadest at the base of the oesophagus, being about 130μ wide; from here it gradually tapers towards the tail end. In the region of the oesophagus the body is more or less cylindrical. Narrow lateral alae are present throughout the length of the body.

The head is triangular in outline and is 30μ high. It is formed of two massive pseudolabia of equal size. Each pseudolabium bears a pair of papillae, one of which is dorsolateral and the other ventrolateral in position. The papillae are typically physalopteroid in form and position. Amphids or lateral organs appear as minute openings situated laterally on the pseudolabia. The mouth opening is flattened and is elongated dorsoventrally. It appears like a long narrow slit. Each pseudolabium bears four teeth on its antero-lateral aspects. One tooth is comparatively large and is borne almost at the tip of the pseudolabium on the externolateral side. This can also be seen in lateral view. The other three teeth are placed in a row internal to the large tooth, on the anterior internolateral sides of each lip. These are not sharply

¹ Manuscript received January 31, 1948.

Contribution from the Institute of Parasitology, Macdonald College (McGill University), Macdonald College P.O., Que.

² Lecturer in Zoology, Muslim University, Aligarh (U.P.), India. (At present at the Institute of Parasitology.)

[The June issue of Section D (Can. J. Research, D, 26:163-196. 1948) was issued July 28, 1948.]

pointed at this stage of the larva. They show a tendency to appear rather like three small lobes of the pseudolabium. This character appears to be important from the point of view of the affinities of the genus *Physaloptera* and may indicate the evolution of the three internolateral physalopteran

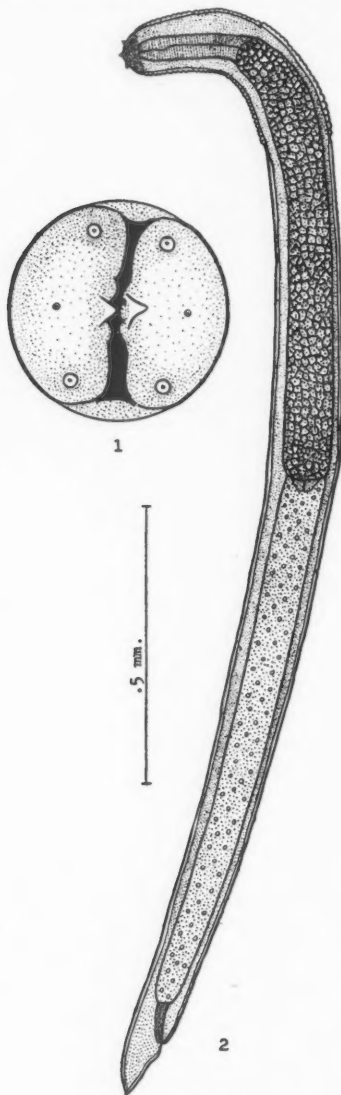


FIG. 1. *En face* view.

FIG. 2. *Lateral* view.

teeth from the trilobed pseudolabia of the other spiruroids, particularly the Gnathostomatidae (2, 3).

The buccal cavity is in the form of a vestibule enclosed by the pseudolabia and is not clearly seen. It is about 30μ deep. The oesophagus extends to the base of the pseudolabia. It is 995μ long and is distinctly divided into two portions. The short anterior cylindrical part is 185μ long by 45μ wide. In the larva under examination, it does not clearly show the development of the muscles, but there can be no doubt that it corresponds to the typical anterior muscular oesophagus of the genus. The posterior part of the oesophagus is very long and broad, being 810μ in length and 90μ in width. The granules in this portion of the oesophagus are heavy and dense, rather coarse and having an alveolar appearance. A lumen can be seen only in the anterior part of the oesophagus. At the posterior end it communicates with the intestine through a pair of valves that appear to be cuticularized.

The intestine originates as a thinner tube than the oesophagus, being only 70μ broad near the start. It communicates posteriorly with a short and narrow rectum, which is 80μ long. No rectal glands are seen. The anus is situated at a distance of 110μ from the posterior end of the body. The tail is conical in form. No papillae or spines are seen on it.

The nerve ring could not be observed. The excretory pore is situated at a distance of about 220μ from the anterior end of the body.

Host: *Labidura repara* (Pallas) (Order: Dermaptera).

Habitat: Body cavity (found free in the body cavity).

Locality: Aligarh (North India).

Discussion

Although the genus *Physaloptera* contains over 50 species from a large variety of hosts including amphibians, reptiles, birds, and mammals, the complete life history of none of them has been worked out up to this time. Seurat (6) gave the description of several third and fourth stage *Physaloptera* larvae from the definitive vertebrate hosts. These descriptions no doubt help to indicate the form of the infective larvae one would expect to find in the intermediate host. Mirza (5) described *Physaloptera* larvae that he found encysted in the body cavity of the Indian squirrel, but whether the latter serves as a proper intermediate host or was an erratic host is not known. Alicata (1) for the first time succeeded in developing the eggs of *Physaloptera* in an intermediate host up to the third stage larvae. He fed the eggs of *Physaloptera turgida* to the cockroach *Blatella germanica*. The worms were taken from an opossum. He states that the first and second stage larvae were found free in the body cavity of the cockroach but the third stage larvae, which took about four weeks to grow, were found encysted in the tissue surrounding the body cavity and were coiled loosely within the cyst. About seven weeks after the initial infection these larvae were found encysted in the body cavity. Alicata states further that some of these "encysted third stage larvae were found to be enclosed in a thin, brownish chitinous-like substance,

probably representing a deposit derived from the tissue of the cockroach. This would probably represent a defense reaction to a foreign invader. . . These deposits appear first usually at the anterior and posterior extremities of the larva, and gradually spread until the larva is enclosed within a tube formed by these deposits. Eventually the larva is killed and becomes completely chitinized." This indicates that *Blatella germanica* can serve as an intermediate host for *P. turgida* but is probably not the natural intermediate host. The infective larvae were fed to a dog, a cat, a rabbit, a guinea pig, a rat, and a chick; these animals were killed and examined after a month but no adults were found in them. Hobmaier (4) developed the eggs of *Physaloptera maxillaris* Molin, also in *Blatella germanica*, up to the infective larval stage. He also states that one or more of these larvae may be found encysted in the body cavity of the cockroach and that "some of these cysts may show a golden brownish colour similar to that of the cuticle of the cockroach, with or without destruction of the enclosed larvae." On feeding the infected cockroaches to cats, dogs, and guinea pigs he did not get any adults.

The larvae described in this paper were found free in the body cavity of the insect. This appears to be the first recorded natural infection of a *Physaloptera* larva in an intermediate host.

References

1. ALICATA, J. E. Larval development of the spirurid nematode, *Physaloptera turgida*, in the cockroach *Blatella germanica*. Papers on Helminthology, Jub. Skrjabin, All-Union Lenin Acad. Agr. Sci., Moscow, 11-14. 1937.
2. CHITWOOD, B. G. and CHITWOOD, M. B. An introduction to nematology. Sec. 1, Part 2. Babylon, N.Y. 1938.
3. CHITWOOD, B. G. and WEHR, E. E. The value of cephalic structures as characters in nematode classification, with special reference to the superfamily Spiruroidea. Z. Parasitenk. 7 : 273-335. 1934.
4. HOBMAIER, M. Extramammalian phase of *Physaloptera maxillaris* Molin, 1860 (Nematoda). J. Parasitol. 27 : 233-235. 1941.
5. MIRZA, M. B. *Sciuris palmarum* als ein interessanter wirt von *Physaloptera* sp. Z. Parasitenk. 6 : 638-641. 1934.
6. SEURAT, L. G. Contribution a l'étude des formes Larvaires des nématodes parasites Hétéroxènes. Bull. Sci. France Belg. 49 : 297-377. 1916.

**CAMERONIA BIOVATA GEN. ET SP. NOV. (THELASTOMATIDAE),
A NEW NEMATODE PARASITE OF THE MOLE CRICKET,
GRYLLOTALPA AFRICANA BEAUV.¹**

BY M. A. BASIR²

Abstract

Cameronia biovata gen. et sp. nov. is described from *Gryllotalpa africana* Beauv. This new genus can be differentiated from the genus *Binema* Trav., 1925, the only genus in the subfamily Thelastomatinae to which it shows some resemblance, by the position of the vulva, which is much posterior in the former, and by its characteristic eggs, which are without polar filaments and are laid in pairs, both the eggs losing their separate identity by fusing with each other along their flattened surfaces, slightly asymmetrically and in a constant and typical pattern.

In his two previous papers (1, 2) the writer has described some new nematodes found as parasites of *Gryllotalpa*. During further study of the same group of insects a new form was met with, which also belongs to the subfamily Thelastomatinae of the family Thelastomatidae. In the opinion of the writer it represents a new genus and a new species of the subfamily Thelastomatinae. The name *Cameronia biovata** is proposed for it.

Description

Genus *Cameronia* gen. nov.

Generic diagnosis: Thelastomatinae.

Male unknown.

Female with mouth opening circular, surrounded by a circumoral elevation and eight labiopapillae. Buccal cavity short and cylindrical, partly surrounded by the oesophagus and containing one dorsal and two subventral cuticular elevations. Oesophagus consisting of a corpus, an isthmus, and a posterior valvular bulb. Excretory pore posterior to base of oesophagus. Tail conical. Vulva in the posterior third of the body. Ovaries two; vagina long and muscular, directed anteriorly. Divergent uteri meet near the middle of body to form a single common uterus, which runs backwards to join the vagina. Eggs elliptical, flattened on one side and fused in pairs along their flattened surfaces, slightly asymmetrically, but in a constant and regular pattern; externally covered by a common cuticular covering; laid in morula stage; polar filaments absent.

¹ Manuscript received April 22, 1948.

Contribution from the Institute of Parasitology, Macdonald College (McGill University), Macdonald College P.O., Que.

² Lecturer in Zoology, Muslim University, Aligarh (U.P.), India. (At present at the Institute of Parasitology.)

* Named after Dr. T. W. M. Cameron, Director, Institute of Parasitology, in recognition of the help the author has continually received from him during his work.

Type species: Cameronia biovata sp. nov.

Specific diagnosis: Cameronia.

Male unknown.

Female 2.35 to 2.50 mm. long by 400μ in maximum width. Cuticle striated throughout the body except the tail. First annule 15μ wide, annules in the cervical region about 7μ apart; towards the middle of the body they increase in width and reach a maximum width of 15μ . Mouth opening circular, surrounded by a circumoral elevation and eight submedian labiopapillae. Buccal cavity short and cylindrical, partly surrounded by the oesophagus, 10μ deep by 10μ wide, and containing one dorsal and two subventral cuticular

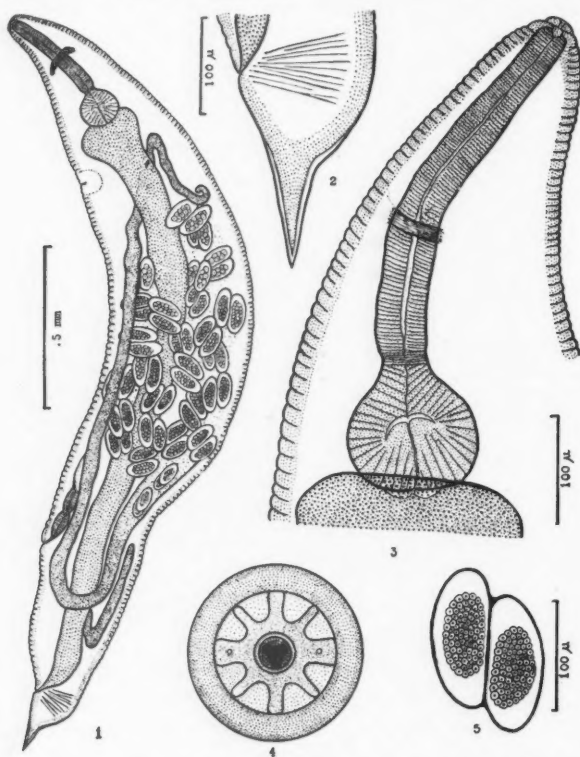


FIG. 1. *Female, entire, lateral view.* FIG. 2. *Female, tail.* FIG. 3. *Female, oesophageal region.* FIG. 4. *Female, en face view.* FIG. 5. *Eggs.*

elevations. Oesophagus 440 to 465μ long, consisting of a corpus 317 to 335μ long by 45μ wide, an isthmus 20μ long by 40μ wide, and a posterior valvular bulb 125 to 150μ long by 230μ wide. Nerve ring 200μ from the anterior end of body. Excretory pore posterior to base of oesophagus, 500μ from the anterior end of body. Intestine enlarged anteriorly to form a cardia. Anus

180 to 190 μ from the posterior end of body. Tail conical. Vulva 1.7 mm, from the anterior end of body, about 72% of the body length from the anterior end. Ovaries two, vagina long and muscular, meeting a common uterus that runs anteriorly up to the middle of body, then branching into two divergent uteri. Eggs elliptical, flattened on one side and fused in pairs along their flattened surfaces with a slight asymmetry, one-fifth of the length of each egg projecting free on opposite sides. Each pair secondarily covered over by a common cuticular layer. Eggs measure 130 μ in length by 50 μ in width, and are laid in the morula stage.

Host: *Gryllotalpa africana* Beauv.

Location: Intestine (rectum).

Type locality: Aligarh (North India).

DISCUSSION

The only genus in the subfamily Thelastomatinae that the genus *Cameronia* resembles is *Binema* Trávassos, 1925 (3, p. 12, Fig. 11 (h); 5, Figs. 1-6). However, it differs from it in the following points. In the genus *Binema* the vulva is described by Trávassos as median in position, while in *Cameronia* it lies in the posterior third of the body. In the former the eggs bear tufts of polar filaments and are laid in capsules, each capsule generally enclosing two eggs or, rarely, three or four. According to Christie (4, p. 250, Fig. 166 (g)) the capsules are "of loose texture formed, apparently, by the entangling and anastomosing of polar filaments," while Valkanov (6) is of the opinion that they are formed as a secondary secretion of the oviduct. In the genus *Cameronia* the eggs have a totally different pattern. They are much bigger in size, being more than double the length of those of *Binema*, and are flattened on one side. They bear no polar filaments, and no capsule of the type described for the genus *Binema* is formed here. The eggs are joined together in pairs by their flattened surfaces, not in complete apposition but with one-fifth of the length of each egg projecting free on opposite sides (Fig. 5). The joining surfaces apparently fuse into each other and the pair is secondarily covered by a layer of cuticular secretion. The eggs thus lose their separate identity and appear as fused in pairs, while in *Binema*, although enclosed in capsules, they remain separate and do not actually fuse with each other.

References

1. BASIR, M. A. Nematodes parasitic in *Gryllotalpa*. Records Indian Museum, 44 : 95-106. 1942.
2. BASIR, M. A. *Chitwoodiella ovofilamenta*, gen. et sp. nov., a nematode parasite of *Gryllotalpa*. Can. J. Research, D, 26 : 4-7. 1948.
3. CHITWOOD, B. G. and CHITWOOD, M. B. An introduction to nematology. Sec. 1, Part 1. Washington, D.C. 1937.
4. CHRISTIE, J. R. An introduction to nematology. Sec. 2, Part 2. Babylon, New York. (Undated).
5. TRÁVASSOS, L. Quelques nématodes du *Gryllotalpa*. Compt. rend. soc. biol. 93 : 140-141. 1925.
6. VALKANOV, A. Über die anatomie und cytologie der nematode *Binema binema* Trávassos. Trav. soc. Bulgare sci. nat. 17 : 153-167. 1936. (In Bulgarian with German summary.)

PARASITES OF FRESHWATER FISH

IV. INTERNAL HELMINTHS PARASITIC IN SPECKLED TROUT (*SALVELINUS FONTINALIS* (MITCHILL)) IN RIVERS AND LAKES OF THE LAURENTIDE PARK, QUEBEC, CANADA¹

BY L. P. E. CHOQUETTE²

Abstract

The distribution and incidence of the following species of helminths from speckled trout in lakes and rivers of the Laurentide Park are recorded: *Crepidostomum cooperi*, *C. farionis*, *Phyllodistomum lachancei*, *Eubothrium salvelini*, diphylobothriid larvae, *Ligula intestinalis*, *Proteocephalus parallacticus*, proteocephalid larva sp. inq., *Rhabdochona laurentiana*, *Metabronema canadense*, *Agamospirura* sp. inq., *Echinorhynchus lateralis*. The sampling includes 42 lakes and streams from seven different drainage systems. The most commonly found species are: *Metabronema canadense*, *Crepidostomum cooperi*, *Eubothrium salvelini*, and *Echinorhynchus lateralis*; these occur in all seven drainage systems. The other helminths vary in their distribution and incidence.

Helminthic infections of freshwater fish in the Province of Quebec have been dealt with in previous papers by Lyster (8) and Miller (12).

The present study of the distribution and incidence of helminthic infection of speckled trout (*Salvelinus fontinalis*) in the Laurentide Park forms a part of the larger study, initiated in 1943, of the biology and parasitology of this fish in the Laurentide area. The work is being carried out in collaboration with the Quebec Department of Fish and Game.

The material under study came mainly from fish collected by field parties from this Institute during the summers of 1945 and 1946; a few specimens were collected during the summer of 1947.

Usually the fish were eviscerated shortly after capture, and the visceral contents examined with the aid of a dissecting microscope; if helminths were present the material was preserved in 5% formalin and sent to the laboratory for more detailed examination. A total of 210 whole fish, preserved in formalin, also was sent to the laboratory for individual examination. Only the findings from these preserved whole fish were used in computing the incidence of infection as given below. Records of some helminthological material collected by the personnel of the Office of Biology, Province of Quebec, during the summers of 1938 and 1939, and sent to this Institute for identification, are also included in this study.

In only one species (*Phyllodistomum lachancei* Choquette) were observations made on living specimens. Alum carmine and Delafield's haematoxylin were

¹ Manuscript received April 22, 1948.

Contribution from the Institute of Parasitology, Macdonald College (McGill University), Macdonald College P.O., Que., with financial assistance from the National Research Council of Canada.

² Lecturer, McGill University and Research Assistant, Institute of Parasitology.

used in the staining of trematodes, cestodes, and Acanthocephala; nematodes were studied after being cleared in lactophenol.

Forty-two lakes and rivers from seven different drainage systems were included in the survey. The lakes and rivers are distributed in the various drainage systems as follows: Chicoutimi, 20; Montmorency, 3; Métabetchouan, 2; Belle-Rivière, 2; Ste-Anne-du-Nord, 3; Malbaie, 2; Jacques-Cartier, 10. As the sampling was done only in summer, no concept of seasonal distribution can be obtained as a result of this investigation. The accompanying map (Fig. 1) shows the configuration of the drainage systems.

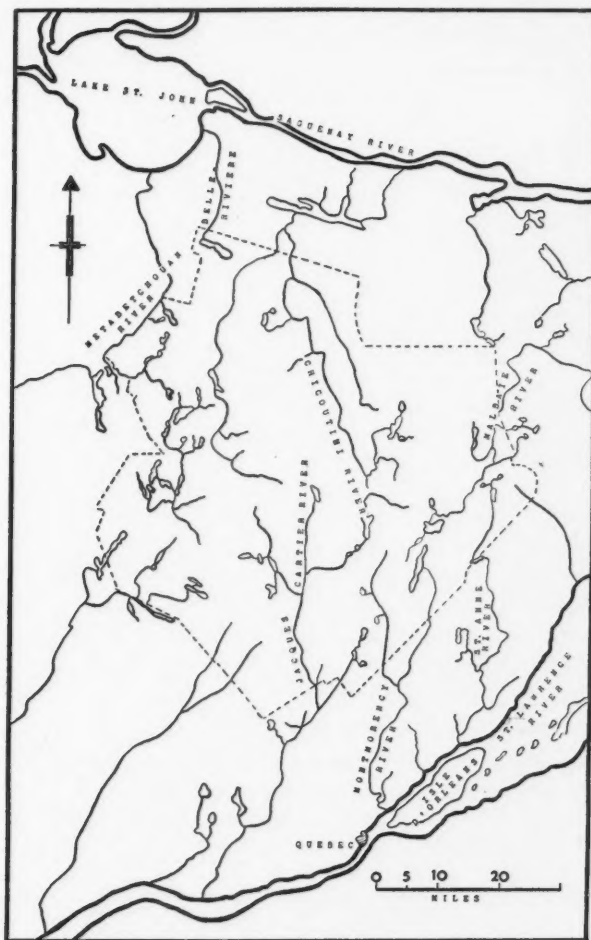


FIG. 1. Configuration of the drainage system.

Distribution and Incidence of Infection

Table I lists the drainage systems in which the various species of parasites were found, together with the number of lakes and streams in each system in which infections were recorded. The detailed records on which this table is based are on file at the Institute of Parasitology.

A brief discussion of the different parasites follows.

TABLE I

Species found and number of lakes or rivers in which it was recorded	Drainage systems*						
	1	2	3	4	5	6	7
	Number of lakes and rivers examined						
	20	10	3	2	2	2	3
<i>Crepidostomum cooperi</i>	16	6	3	1	2	2	2
<i>C. farionis</i>	0	2	1	0	0	0	0
<i>Phyllodistomum lachancei</i>	0	2	1	0	0	1	1
<i>Eubothrium salvelini</i>	12	7	1	2	2	2	1
<i>Ligula intestinalis</i>	1	0	0	0	0	0	0
<i>Proteocephalidae</i> sp.	3	5	1	0	0	0	0
<i>Diphyllbothriid</i> larvae	7	4	1	0	1	0	1
<i>Metabronema canadense</i>	20	9	3	2	2	2	2
<i>Rhabdochona laurentiana</i>	3	1	0	0	0	0	0
<i>Agamospirura</i> sp. inq.	3	2	0	0	0	0	1
<i>Echinorhynchus lateralis</i>	13	6	1	1	2	2	2

* Chicoutimi River = 1 Belle-Rivière = 5
 Jacques-Cartier = 2 Malbaie = 6
 Montmorency = 3 Ste-Anne-du-Nord = 7
 Métabetchouan = 4

Trematodes

Two species of the genus *Crepidostomum* (Allocreadiidae) and one of the genus *Phyllodistomum* (Gorgoderidae) were recorded. "Black spot" was found to be widely but erratically distributed throughout the area studied. A separate account of the distribution of this condition is in preparation. Lyster (9) in 1940, working in another area of the Laurentian mountains in Quebec, showed that it is caused by the trematode parasite *Apophallus brevis*.

Genus *Crepidostomum* Braun, 1900

Of the two species of *Crepidostomum* recorded from trout, *C. cooperi* is the more prevalent in this area. It was found in fish from all seven drainage systems. It was found in 107 of the 210 fish examined individually. While it usually lives in the intestine and the pyloric caeca, in several instances it was found in the gall bladder and stomach. *C. farionis* (Fig. 2) does not seem to have as wide a distribution as *C. cooperi*. It was recorded from fish of three lakes: Lac Horatio Walker and Lac Sept-Isles of the Jacques-Cartier river system, and in Lac des Roches of the Montmorency river system.

Species of *Crepidostomum* have been reported by other workers from Quebec and Ontario. The earliest report is that of Stafford (16) whose findings have been commented upon by Nicoll (Hunninen and Hunter (6)),

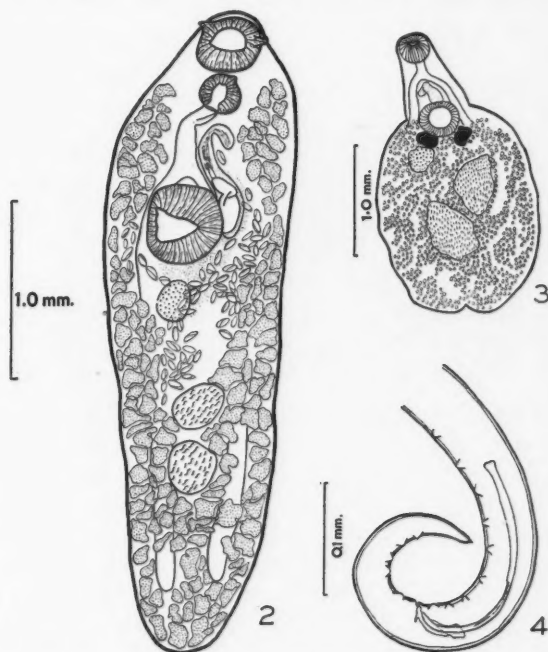


FIG. 2. *Crepidostomum farionis*, ventral view.

FIG. 3. *Phyllodistomum lachancei*, ventral view.

FIG. 4. *Rhabdochona laurentiana*, posterior extremity of male.

Hopkins (5), and Miller (13). Richardson (14), in 1936, recorded *C. cooperi* (under the name of *C. fausti*) from Lake Edward, Champlain County, Que. Lyster (8) found *C. cooperi* in speckled trout from Lake Commandant. The only other records of *C. farionis* in this country are those of Bangham and Venard (1), and MacLulich (11) who recorded it from speckled trout in the Algonquin Provincial Park in Ontario.

Genus *Phyllodistomum* Braun, 1899 (Fig. 3)

Only one species of *Phyllodistomum* was found in trout. The trematode occurred in the ureters of the host, always in small numbers, not more than eight individuals being present in any one fish. This trematode proved to be a previously undescribed species, and was described and named *Phyllodistomum lachancei* by the author (4). Sections of the ureters and kidneys of the parasitized fish show that the pathological changes caused by the parasite consist of a marked enlargement of the ureteral lumen and a flattening of the

lining columnar epithelial cells. No evidence of damage to the parenchymal tissue was found. This parasite was found in two lakes of the Jacques-Cartier river drainage (Lac à Regis and Lac Horatio Walker), in Lac Carré of the Malbaie system, in Lac des Roches of the Montmorency system, and in Lake Turgeon of the Ste-Anne-du-Nord drainage.

Cestodes

Eubothrium salvelini (Schrank, 1790)

The systematic position of species of this genus in Canadian fish has been discussed by Wardle (19) and Kuitunen-Ekbaum (7). *E. salvelini* has been recorded from trout in other parts of the province by Richardson (14), and Lyster (8). It was also recorded by MacLulich (11) and Bangham and Venard (1) from Ontario.

Mature and immature forms were found in 60 of the 210 fish examined. In most cases the worms were located in the pyloric caeca and to a lesser extent in the intestine; a few specimens were also found in the stomach. This cestode was prevalent in fish from all seven drainage systems.

Diphylobothriid larvae

Although these were the larval cestodes most commonly encountered, only 11 fish out of the 210 examined, were infected. They were found encysted on the outer surface of the stomach, intestine, and kidney, but in small numbers only in any one host. The infection was found in five of the drainage systems, namely: Chicoutimi, Jacques-Cartier, Montmorency, Ste-Anne-du-Nord, and Malbaie. MacLulich (11), in a similar survey of the lakes in Algonquin Park, does not record the presence of these forms in speckled trout.

Ligula intestinalis (Linn. 1758)

This species was found only once, in the body cavity of a trout from the River Chicoutimi. This finding constitutes the only record of the parasite in the speckled trout in Canada.

Proteocephalidae (syn. *Ichthyotaeniidae*)

Larval stages and immature adults of proteocephalid cestodes were found in the intestine of a small number of fish in a few lakes from the Chicoutimi, Jacques-Cartier, and Montmorency drainage systems. The immature adults were, on the basis of the characters exhibited by the vagina in its relationship to the cirrus pouch, identified as *Proteocephalus parallacticus* as described by MacLulich (10). However, in other lakes in these three drainage systems larval stages of members of this family were found but these could not be identified as to species. They occurred only in very small numbers. As pointed out by Van Cleave and Mueller (17), the presence of such larvae is of common occurrence in fish that cannot bring them to maturity. Lyster (8) records such larvae in speckled trout from Lake Commandant.

Nematodes

Nematode infections of trout in this area are represented by one species of the Thelaziidae and one adult and one larval species of Spiruridae. This type of infection resembles closely that encountered by Lyster (8) in other parts of the province. It is quite different from those encountered by Bangham and Venard (1) and MacLulich (11) in the Algonquin Park, and none of the species recorded here was found by Richardson (14) in his study of the parasites of speckled trout.

Rhabdochona laurentiana Lyster, 1940 (Fig. 4)

This species was seen in a few fish from lakes of the Chicoutimi and Jacques-Cartier drainage systems, but was present in very small numbers in any one fish. Lyster (8) described it originally from Lake Commandant, Quebec.

Metabronema canadense Skinker, 1931

Skinker (15) described this species from speckled trout taken in the River Matamek, Quebec Province. This nematode was the helminth most commonly encountered during this survey and was collected from 139 of the 210 fish examined. The parasite was found usually in the stomach, less frequently in the pyloric caeca and intestine.

Lyster (8) recorded *Metabronema* (= *Cystidicola*, *Cystidicoloides*) *harwoodi* from the same host in another part of the province. This species was originally described by Chandler (3) from speckled trout. However, re-examination of Lyster's type material showed it to be identical with *M. canadense*.

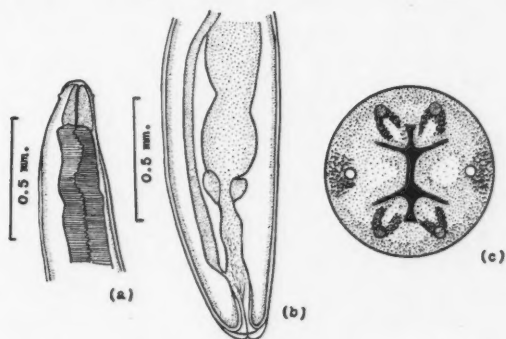


FIG. 5. *Agamospirura* sp. inq.

- (a) Lateral view of anterior extremity.
- (b) Posterior extremity.
- (c) Sketch of cephalic pattern.

Agamospirura sp. (Fig. 5, a, b, c)

Eleven immature spirurids were found in fish taken during the summer of 1945 and 1946, and in material collected by personnel of the Office of Biology in 1939. One of these larvae was found encapsulated on the external

surface of the stomach wall, others were found in the flesh, the ovaries, the pyloric caeca, the swim bladder, and the body cavity. They were collected from fish from lakes and rivers of the Chicoutimi, Jacques-Cartier, and Ste-Anne-du-Nord drainage systems.

The worms are cylindrical, brownish in color, 25 to 34.5 mm. in length. The cuticle is thick and transversely striated. The anterior extremity when viewed laterally is conical in outline; *en face* view of the head shows that the mouth opening is elongated dorsoventrally and flanked by two trilobed pseudolabia of which the lateral lobes are the larger. There are four submedian papillae located on the base of the pseudolabia. This arrangement suggests that the dorsodorsal-laterodorsal and ventroventral-lateroventral papillae have become fused. The internal circle of papillae is apparently absent.

Cervical papillae are present, located 0.037 to 0.04 mm. from the anterior extremity. The width of the anterior extremity at the level of the cervical papillae is 0.131 to 0.149 mm. The mouth is followed by a single vestibule, 0.125 mm. in length by 8μ in diameter. The oesophagus following the pharynx is from 8 to 9 mm. long and divided into an anterior muscular portion and a posterior glandular portion that is about six times as long as the muscular one. Both parts of the oesophagus are traversed by a strong oesophageal tube. The intestine is irregular in outline and difficult to follow; it terminates in a chitinous rectum averaging 0.725 mm. in length. At the level of its junction with the intestine, conspicuous glands could be seen. The anus is terminal. Neither the excretory pore nor the nerve ring was seen in any of the specimens. In two of the immature forms there were traces of growth of the male genital rudiment.

The structure and characters of the cephalic extremity are considered to be sufficient to class these immature forms as Spiruridae and, more specifically, as being representative of the subfamily Spirurinae as defined by Chitwood and Wehr (2).

Acanthocephala

A single species belonging to the genus *Echinorhynchus* was found. It was tentatively identified as *E. lateralis* Leidy, 1851, from the description given by Richardson (14) of forms he found in speckled trout in Lake Edward, Que. Some of the present specimens were sent to Prof. Van Cleave who found them (18) to be identical with specimens that Richardson had previously sent him.

This species is widely distributed in the area and was recorded from all the drainage systems studied. They were found in 55 of the 210 fish examined; they were chiefly in the intestine although many were also in the pyloric caeca.

References

1. BANGHAM, V. and VENARD, C. E. Parasites of fish of Algonquin Park lakes. Publications of the Ontario Fisheries Research Laboratory, 65 : 33-46. 1946.
2. CHITWOOD, B. G. and WEHR, E. E. The value of cephalic structures as characters in nematode classification, with special reference to the superfamily Spiruroidea. Z. Parasitenk. 7 : 273-335. 1934.

3. CHANDLER, A. C. New genera and species of nematode worms. Proc. U.S. Natl. Museum, 78 (Art. 23) : 1-11. 1931.
4. CHOQUETTE, L. P. E. *Phyllodistomum lachancei* sp. nov., a trematode from the ureters of *Salvelinus fontinalis* (Mitchill), with a note on its pathogenicity. Can. J. Research, D, 25 : 131-134. 1947.
5. HOPKINS, H. S. The papillose Alloecreadiidae. Ill. Biol. Monographs, 12 : 1-80. 1934.
6. HUNNINEN, A. V. and HUNTER, G. W. III. On the species of *Crepidostomum* in trout. Trans. Am. Microscop. Soc. 52 : 150-157. 1933.
7. KUITUNEN-EKBAUM, E. A study of the cestode genus *Eubothrium* of Nybelin in Canadian fishes. Contrib. Can. Biol. Fisheries, 8 : 90-98. 1933.
8. LYSTER, L. L. Parasites of freshwater fish. II. Parasitism of speckled and lake trout and the fish found associated with them in Lake Commandant, Que. Can. J. Research, D, 18 : 66-78. 1940.
9. LYSTER, L. L. *Apophallus imperator* sp. nov., a heterophyid encysted in trout, with a contribution to its life history. Can. J. Research, D, 18 : 106-121. 1940.
10. MACLULICH, D. A. *Proteocephalus parallacticus*, a new species of tapeworm from lake trout, *Cristivomer namaycush*. Can. J. Research, D, 21 : 145-149. 1943.
11. MACLULICH, D. A. Parasites of trout in Algonquin Provincial Park, Ontario. Can. J. Research, D, 21 : 405-412. 1943.
12. MILLER, M. J. Parasites of freshwater fish. III. Further studies on the internal trematodes of fish in the central St. Lawrence watershed. Can. J. Research, D, 18 : 423-434. 1940.
13. MILLER, M. J. A critical study of Stafford's report on "Trematodes of Canadian Fishes" based on his trematode collection. Can. J. Research, D, 19 : 28-52. 1941.
14. RICHARDSON, L. R. Observation on the parasites of the speckled trout in Lake Edward, Quebec. Trans. Am. Fisheries Soc. 66 : 343-356. 1936.
15. SKINKER, M. S. Three new parasitic nematode worms. Proc. U.S. Natl. Museum, 79 (Art. 24) : 1-9. 1932.
16. STAFFORD, J. Trematodes from Canadian fishes. Zool. Anz. 27 : 481-495. 1904.
17. VAN CLEAVE, H. J. and MUELLER, J. F. Parasites of Oneida Lake fishes. Part 3. A biological and ecological survey of the worm parasites. Roosevelt Wild Life Ann. 3 : 1-334. 1934.
18. VAN CLEAVE, H. J. Personal communication. 1947.
19. WARDLE, R. A. The cestoda of Canadian fishes. II. The Hudson Bay drainage system. Contrib. Can. Biol. Fisheries, 7 : 379-403. 1932.

THE FUNCTION OF THE GIANT AXON OF *MYXICOLA INFUNDIBULUM* MONTAGU¹

By J. A. COLIN NICOL²

Abstract

The polychaete, *Myxicola infundibulum*, contains a very large nerve fiber that runs throughout the nerve cord and gives off peripheral branches to the longitudinal muscles. Movements of the animal are quick synergic contractions of the whole body and slower metachronous locomotory movements. Injury to the giant axon without interrupting the rest of the nerve cord blocks the passage of the quick contraction but not of slower locomotory waves. It is concluded that the quick end-to-end shortening is intermediated by the giant axon and that slow waves of movement depend upon transmission through short segmentally linked neurones. Traction of one segment on another is not effective in transmitting either type of movement. The giant fiber response is of an all-or-none nature. Repetitive stimuli lead to summation of muscular contractions. The axon conducts in either direction during the natural life of the animal. The nature of the effective stimuli, the simplicity of the neuronal arrangement involved, and the character of the synergic response are discussed in terms of their survival value to the species.

Introduction

There are a considerable number of experimental studies dealing with the giant nerve fibers of lumbricids, and certain aspects of their function are now well known, but few investigators have concerned themselves with the functioning of the giant fibers of polychaetes. Friedländer (11) suggested that the three dorsal giant axons of the earthworm were involved in the 'startle' reaction or end-to-end shortening in which the animal suddenly contracts in length when disturbed and this hypothesis has since been confirmed by several investigators. Bovard (2) made a rather ingenious approach to the problem when he showed that following section of the nerve cord of the earthworm the giant axons regenerated and grew together more slowly than the rest of the cord. Correlated with this fact he found a corresponding delay in the return of quick end-to-end contractions throughout the length of the worm, in contrast to the quicker return of co-ordination of slower locomotory movements. Yolton (27), Stough (25), and ten Cate (26) subsequently confirmed these observations by sectioning the giant axons of the earthworm without interrupting the rest of the nerve cord, and they showed that the end-to-end contraction failed to pass from one part of the body to the other across the lesion, thus clearly indicating that the giant nerve fibers intermediate this response.

The giant axons of many polychaetes attain even greater dimensions than in oligochaetes and, moreover, some species of polychaetes show the same kind of end-to-end shortening as the earthworm. It has been suggested frequently, therefore, that the giant axons of polychaetes have the same

¹ Manuscript received April 9, 1948.

Contribution from the Department of Zoology, The University of British Columbia, Vancouver, B.C.

² Assistant Professor of Zoology.

function as those of the earthworm but no conclusive evidence has ever been presented for this correlation. I have recently made a study of the structure of the giant nerve fibers of several species of sabellids (18) and in the course of that investigation some evidence was obtained for the functioning of the giant axon of *Myxicola infundibulum* Montagu. The several aspects of the problem that presented themselves may be treated as follows: (1) does the giant axon of *Myxicola* intermediate the quick end-to-end contraction of this animal; (2) is it concerned with any other movements of the animal; (3) what is its position in the nervous pathway in which it occurs and does it possess any physiological polarity in the intact animal comparable to the law of forward direction of vertebrate neurones?

Structure of the Giant Axon of *Myxicola*

Several authors have commented on the extraordinarily large size of the giant axon of *Myxicola infundibulum* (7, 8, 21) and these earlier accounts have been confirmed in part and augmented by recent communications (18, 19). A single large axon runs throughout the length of the nerve cord, beginning in the suboesophageal ganglion in setiger II. This axon subdivides into two fibers on several occasions in the first few segments (setigers II to IV) and sends a branch up each oesophageal connective into the supraoesophageal ganglia where the two branches terminate, independently of each other, in a pair of relatively large nerve cells. The giant axon also is connected with numerous nerve cells throughout its length in the nerve cord and since it is a continuous structure without internal dividing septa or 'macrosynapses' it constitutes a syncytial neurone. It varies considerably in size in different animals and in different states of contraction or extension, having a greater diameter in larger individuals, and increasing about twofold in diameter during contraction and shortening of the worm. It also varies in diameter along its length. In mature specimens representative axon diameters are about 500 to 1000 μ in the thorax and anterior abdomen, followed by a gradual decrease to 100 μ or less in the posterior abdomen. A transverse section through the anterior third of the body reveals that nearly all the nerve cord is occupied by the giant nerve fiber and it constitutes about 33% of the entire volume of the cord. About eight large peripheral branches arise from the nerve cord in each segment and these peripheral branches enter the body wall and extend towards the mid-dorsal line, giving off small collaterals along their course to the longitudinal muscle fibers. The giant fiber branches run parallel to one another without apparent anastomoses in the periphery of the body. The giant axon, therefore, is not only a large syncytial structure lying within the nerve cord, but it also extends into the body wall and envelops and penetrates the entire longitudinal musculature of the animal (Figs. 1, 2, 3).

The longitudinal muscles of *M. infundibulum* are very strongly developed and form four massive and symmetrically arranged areas, two dorsal and dorsolateral, separated from each other by the dorsal medial mesentery, and two ventrolateral, separated by the median nerve cord.

Behavior of *M. infundibulum*

M. infundibulum is a cosmopolitan species about 13 cm. long. It consists of a ciliated feeding crown at its anterior end and a trunk of about 130 segments bearing short chaetae and uncini but no parapodia. It lives in a bulky mucous tube buried in sand and clay near low tide mark and extends its crown and anterior segments from its tube in order to feed.

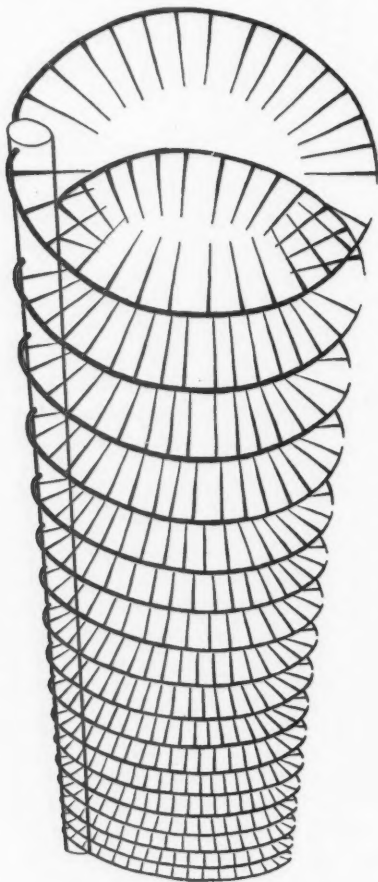
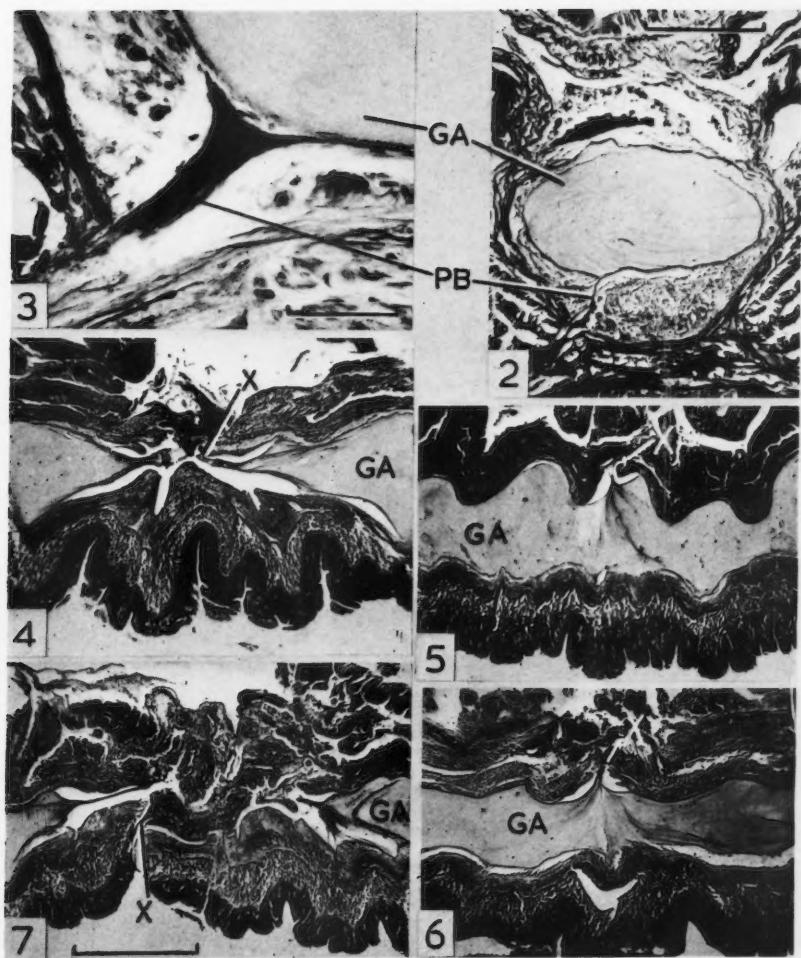


FIG. 1. Diagram of the giant axon of *Myxicola infundibulum*, showing peripheral branches that extend into the body wall.

The surprisingly quick and powerful contraction of this species has been noted by a number of observers (6, 17) and Friedländer (11) stated that it showed very little activity apart from this quick shortening. He noted, moreover, that when the nerve cord was cut across the quick contraction

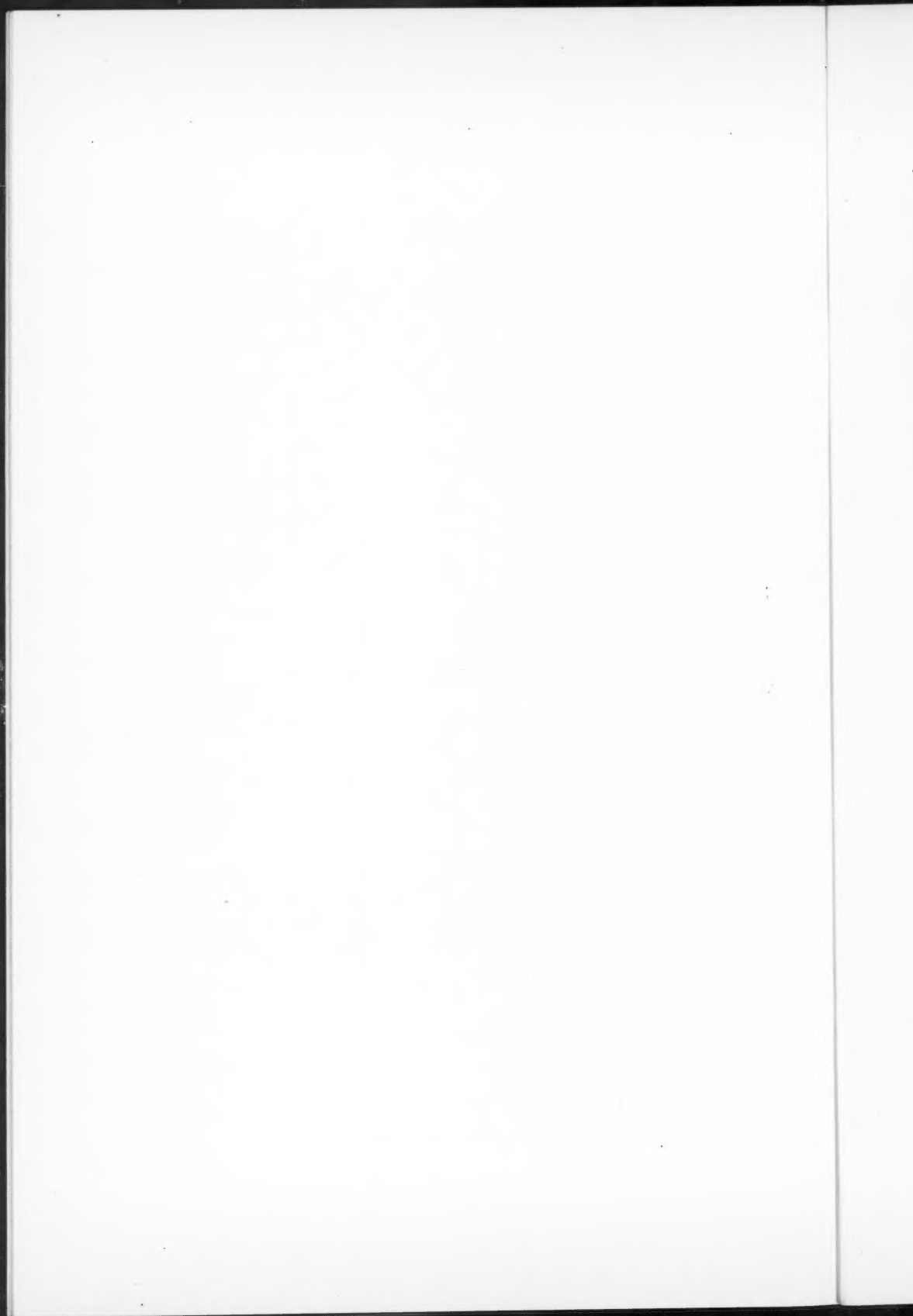


FIGS. 2 to 7. Photographs of sections through the nerve cord and giant axon of *Myxicola infundibulum*.

FIG. 2. Transverse section through the nerve cord, showing a peripheral branch arising from the left ventrolateral region of the giant axon. FIG. 3. A more highly magnified view of the origin of a peripheral branch. Silver impregnation (Holmes' method). FIGS. 4 to 7. Longitudinal sections through the nerve cord of operated animals. Ehrlich's haematoxylin and eosin.

Legend.—GA, giant axon. PB, peripheral branch of giant axon. X, site of transection of giant axon (and nerve cord).

Magnifications indicated by horizontal lines: in Figs. 2 and 3, equivalent to 250 μ ; in Figs. 4 to 7, equivalent to 1 mm. (shown on Fig. 7 only).



did not pass the injured segment to the part of the body beyond, but since the smaller fibers of the neuropil as well as the giant axon are transected in such an operation it does not in itself offer proof of the function of the giant axon.

If a worm is removed from its tube and placed in a dish of sea water it slowly elongates and opens its crown. If any part of the body is touched it gives a single quick contraction and closes its crown. If subjected to a series of tactile stimuli it responds by a series of quick contractions, one per stimulus, and vigorous and repeated tactile stimuli will cause the animal to shorten to about one-third of its extended length into a short and rigid cone. The animal shows some kind of adaptation to tactile stimulation since it ceases to give quick contractions after about the eighth stimulus. On cessation of stimulation, subsequent elongation of the worm and opening of the crown occupy from 5 to 10 min.

The animal also shows several other types of movement. In a dish containing sea water it slowly moves backwards by means of antiperistaltic waves originating at the posterior end; the tail also is in constant exploratory movement, slowly moving about the substratum. On a floor of sand it initiates burrowing by slow forward and backward movements of its tail and soon covers itself with sand. Slow peristaltic waves are rather difficult to follow by eye but they can be accentuated and clearly watched following chemical stimulation. When a drop of concentrated hydrochloric acid is dropped into the water above the tail of the animal it gives a series of quick contractions, followed by a succession of antiperistaltic waves of thickening and thinning originating near the posterior end and passing forwards over the posterior third of the animal. As a result the posterior end is kept retracted from the region of stimulation. When a drop of acid is dropped above the crown, on the other hand, the animal gives one or more quick contractions, the anterior half of the body is kept retracted, but the posterior end soon elongates and begins exploratory movements. The result, again, is that the stimulated region is retained away from the source of stimulation. Swimming and lashing movements have never been observed, although they do occur rarely in the allied species, *Branchiomma vesiculosum* Montagu.

The quick shortening can be elicited by several types of stimuli. The first one that has been mentioned is tactile stimulation. Touching any part of the body, say with a blunt seeker, causes the animal to contract. The most sensitive areas to tactile stimulation are the crown, head, and tail while the intervening trunk appears to be less sensitive. Stimulation of the crown gives a rough guide to the intensity of stimulation necessary to evoke a response. Gentle depression of one of the pinnules is without effect or results in slight folding of the crown only; more vigorous deformation of one or more pinnules calls forth a quick contraction. The second type of stimulus causing a quick contraction is vibration of the substratum. Jarring the table, say by setting down another container, causes all the animals to contract and close their crowns. Currents created by agitating the water also lead to end-to-end

shortening. The third effective stimulus is some noxious chemical agent like strong acid. Finally, sudden change in light intensity occasionally elicits a quick shortening movement but this stimulus is not uniformly effective. It causes a response in only some of the animals in any one container and only occasionally and erratically in the case of any one specimen. In this respect *Myxicola* differs from some other species of sabellids and serpulids in which the light reflex is strongly developed, for example *Branchiomma vesiculosum* and *Hydroides dianthus* (16).

It is probable that the behavior of *Myxicola* is more complex than the responses described above would indicate but this description serves at least to delimit some of the characteristic behavioral patterns of the animal for immediate exploration. In general we find that the responses of *Myxicola* are of two types: (1) quick end-to-end synergic contractions of the massive longitudinal musculature; (2) slower metachronous locomotory waves. In the nervous system we find two sharply distinguishable categories of neurones: (1) a large continuous giant axon extending throughout the nerve cord; (2) small segmentally arranged neurones forming short pathways. Evidence will now be presented that the giant axon mediates the end-to-end contractions.

Effect of Cutting the Nerve Cord and the Giant Axon

Since the giant axon of *Myxicola* is so large an opportunity is afforded of transecting it easily without damaging the rest of the nerve cord and this operation has been performed upon several specimens. Healthy worms were chosen that exhibited the quick contraction throughout their length. The animal was cut open dorsally by a slit 1 to 2 cm. long, the gut removed from the exposed region and the body wall pinned out in a dissecting dish under sea water. The giant axon, clearly visible, was then cut across with a sharp-pointed scalpel, care being taken not to transect the underlying neuropil of the cord at the same time. Reactions of the animal were noted, after which the operated region was prepared for histological examination. The specimens were fixed in Bouin's fluid made up in sea water, double-embedded in celloidin-paraffin, and cut longitudinally at 15μ as serial sections, which were stained with Ehrlich's haematoxylin and eosin. The protocols of these experiments follow. In each case the giant axon was cut in the anterior abdominal region.

Specimens Nos. 601, 607, 610

In these three specimens the giant axon alone was transected. The following responses were observed after operation. Sharp mechanical stimulation of the anterior end resulted in a quick contraction that proceeded only as far as the injured region. But after a brief interval a progressive wave of thickening proceeded along the abdomen posterior to the injured region. On mechanical stimulation of the posterior end the region posterior to the lesion gave a quick contraction that did not extend in front of the operated region. A slow contraction sometimes occurred in the anterior region of the body

following posterior stimulation. Pinning down the body wall over a length of several segments in the operated region produced no change in the movements described.

Histological Picture

Sections showed that in each specimen the giant axon was injured while the ventral region of the cord was intact (Figs. 4, 5, 6). In each specimen axoplasm had escaped into the coelomic cavity. There were, however, individual differences in the extent of the injury to the giant axon. In only No. 610 was there complete division of the giant axon; in Nos. 607 and 608 the axon was only partially transected. It has been observed previously (18) that the axoplasm of the giant fiber of this species is viscous and shows little tendency to flow. Consequently, it is not surprising that a transverse cut should result in little loss of axoplasm and, in two specimens, only partial interruption of axoplasm.

No. 609

This specimen represents one of many in which the entire nerve cord was cut. Stimulation of either the anterior or posterior end gave rise to quick contractions, followed by slower waves of thickening. These movements were confined to the portion of the body stimulated, that is, they were always proximal to the lesion: in no case did either quick contractions or slower waves leap over the operated region.

Histological Picture

The giant fiber was interrupted and axoplasm had escaped into the coelomic cavity. In addition, the rest of the nerve cord and the body wall in the mid-ventral line were cut through (Fig. 7).

It may be concluded from these experiments that the giant axon is responsible for intermediating the quick shortening movement of *Myxicola* since interruption of the axon alone blocks the passage of this contraction across the injured region. The experiments show also that the nerve cord is concerned with the passage of slow metachronous movements along the length of the animal and that transmission of these movements cannot take place by pull or traction of one segment or region on successive segments.

Effect of Cutting the Lateral Body Wall

The following operation was performed to determine whether there are any anastomoses among the branches of the giant axon peripherally in the body wall. The ventral body wall was cut through longitudinally on one side, over a length of 5 to 10 segments, parallel to the nerve cord. The animal was then stimulated mechanically to cause the giant fiber response. Longitudinal contraction normally leads to shortening and swelling of each segment. The resultant quick contraction after this operation involved the entire length of the body with the exception of the body wall lateral to the incision. This was apparent from the fact that the animal curved outwards during contraction

towards the injured side. Dorsal to the cut the segments remained expanded and became narrower towards the mid-dorsal line. Since the peripheral branches of the giant axon were cut ventrally by this operation but were left intact dorsally, it may be concluded that these peripheral axons do not fuse with one another either dorsally, across the mid-line of the body, or longitudinally, successive branches with one another. These observations support the appearance seen in histological sections in which each peripheral branch of the giant axon remains discrete in the body wall and forms a half-ring on one side of the body (Fig. 1).

Giant Axon Contractions

A preliminary analysis of giant axon contractions of *Myxicola* has been made, using electrical stimuli. Condenser discharges were used and stimuli were applied by Ag-AgCl electrodes (14). The latter were suspended in glass tubing containing sea water. The narrow mouths of the tubes, about 4 mm. apart, were placed on the skin of the animal beneath the surface of the sea water. Kymograph records were made for purpose of measurement.

A single electrical stimulus, above threshold, causes a single vigorous contraction of the animal. This sharp contraction occupies about two seconds and is followed by slow elongation, sometimes interrupted by small contractile waves. A contraction may be produced by stimulating any part of the body except the distal half of the branchial crown. This suggests that the current is stimulating the giant axon directly and not via peripheral sensory neurones since the giant axon terminates in the supraoesophageal ganglia but can be fired by mechanical stimulation of the branchial crown. Moreover, if the anterior half of the animal is anaesthetized by immersion in 6% magnesium chloride for 15 min., tactile stimulation of this region is usually ineffective while an electrical stimulus always causes a quick contraction.

A series of spaced stimuli (from 1 to 40 stimuli per minute) produces a series of discrete contractions, one per stimulus. Stimulation at any one position over a given period (usually about 10 min. gives a series of consistent results) shows that the shortening response is of an all-or-none nature. Under these conditions and with constant potentiometer setting, successive contractions are nearly the same height. When stimulation is subthreshold there is no movement apart from slight swelling of the body wall immediately below the electrodes. A threshold stimulus produces one contraction while increase in stimulus strength produces no change in the height or type of response. Repetitive threshold or suprathreshold stimuli, at increasing frequency, result first in clonus- and then in tetanus-like contractions.

Although single subthreshold stimuli (frequency one every 10 sec.) are ineffective in causing a contraction, it is possible to obtain summation of two individually inadequate stimuli by excitation at shorter intervals. The range explored was 0.56 to 10 sec. intervals, of which 0.56 sec. to five seconds were effective in summation. The long effective period of facilitation (up to five seconds) with two subthreshold stimuli would seem to indicate that summation

can occur in the epidermal receptors (not discounting the possibility that summation occurs in the giant axon itself at shorter intervals). This observation, in conjunction with the necessity of applying vigorous tactile stimuli to the pinnules of the crown, mentioned above, suggests that the giant axon can be fired normally as the result of temporal and spatial summation in the afferent pathways.

Discussion

The giant axon of *Myxicola* conducts impulses causing the quick end-to-end contraction of the entire animal and therefore has a function similar to that of the three giant axons of the earthworm but it differs from the latter in one important respect, viz., in its lack of functional polarity. In the earthworm, despite the presence of segmentally arranged macrosynapses, the giant axons are capable of conducting in either direction as the result of electrical stimulation (9) but in the intact animal the median giant usually conducts impulses largely anteroposteriorly following tactile stimulation of the anterior end of the body and the two laterals posteroanteriorly following tactile stimulation of the posterior region (5, 23, 25). Rushton (23) and Stough (25) believe that this difference in conduction direction results from differences in the sensory connections of the median and lateral fibers in the anterior and posterior regions of the worm. Rushton (22) found significant differences in the kind of end-to-end contractions resulting from anterior and posterior stimulation, respectively. Bullock (5) has shown also that in *Neanthes virens*, which has five giant axons (15), the giant fibers conduct equally well in either direction along the length of the worm as the result of electrical stimulation. In this species, however, the median giant fiber is fired by tactile stimuli in the anterior quarter, the pair of mediolateral giant fibers by tactile stimuli in the posterior three-quarters, and the two large lateral giant axons by stronger stimuli at all levels. The giant fiber system of *Neanthes* thus resembles that of *Lumbricus* in certain features of functioning as well as in the presence of inter-segmental macrosynapses (24). Since the giant axon of *Myxicola* is a continuous structure, no complications are introduced by the presence of transverse septa and *ex hypothesi*, from the bases of the neurone doctrine, it would be expected to conduct an impulse, originating in any part of its length, throughout its extent in the nerve cord and body wall. It is of interest, however, that it is capable of being excited by tactile stimulation in any part of the body and consequently transmits impulses in either direction along its length in the natural life of the animal.

Afferent fibers from the coronary nerves enter into the formation of the dense neuropil which surrounds the two giant fiber nerve cells in the supra-oesophageal ganglia, and afferent fibers from the epidermal receptors in each segment form a complex feltwork immediately beneath the giant axon in the nerve cord. The histological picture suggests that the reflex arc involved in the giant fiber response is a comparatively simple one, of sensory neurones making direct contact with the giant axon, and of the giant axon itself constituting the efferent side of the arc. The giant fiber, in its role of an efferent

axon traversing the entire central nervous system and directly innervating all the longitudinal muscle fibers of the trunk, constitutes a unique example of an initial and a final common path for a synergic response. The two most striking features of this arrangement are (1), the simplicity of the afferent path in which sensory neurones, with short centripetal course, are capable of firing the giant axon at all points and (2), the simplicity of the efferent side of the arc with a single long distance fiber lying in the central nervous system and itself directly innervating the major muscle mass of the body.

There is no evidence that the giant axon is concerned with any other type of movement besides the shortening reaction of the animal since variation in intensity and frequency of stimulation produces either one or a series of similar sharp contractions. The giant axon is not necessary for the propagation of slower locomotory and contractile waves since these are not stopped by section of the giant axon but are interrupted by section of the entire nerve cord. In the earthworm slow locomotory waves can be transmitted along the body of the animal even when pieces of the cord are removed, by traction of one segment on another (1, 10, 12). Quick end-to-end contractions are not transmitted by this means in earthworms. In *Nereis* on the other hand (3, 13), section of the nerve cord abolishes all co-ordination of locomotion between the two halves of the body. *Myxicola* resembles *Nereis* in this regard in that pull of one segment on another is not effective in transmitting the quick contraction or locomotory waves along the body. The actual rate at which these slow waves of thickening and thinning are propagated has not been measured but they can be followed easily with the eye as they course slowly over the surface of the animal; their velocity is very slow and is of the order of a few centimeters per second. Bovard (1) gives a mode of 25 mm. per second for the transmission of locomotory impulses in the earthworm. The low rate in *Myxicola* suggests that transmission is effected by means of neuronal chains, with consequent synaptic delay in each segment, and not by continuous axons extending long distances in the cord.

Confirmation of some of these results has since been obtained by Nicol *et al.* (20, pp. 243-244) who have recorded giant fiber action potentials from the dissected nerve cord and from intact specimens of *Myxicola*. In this investigation it has been found that the giant axon conducts in either direction as the result of electrical and tactile stimulation and that single stimuli, electrical or tactile, give rise to single action potentials, one for each stimulus. Each giant fiber action potential is followed in turn by a single muscle potential, corresponding to the synergic contraction of the longitudinal muscles of the trunk (making allowance, of course, for conduction time). These observations supplement those reported in the present communication in that they demonstrate that each quick contraction of the animal is caused by a single all-or-none impulse in the giant axon.

It is possible to recognize many features of survival value to the animal in the arrangement and functioning of the giant fiber system of *Myxicola*. The saving of conduction time that results from the large diameter of the axon

and the continuity of the efferent pathway has already been noted (18). *Myxicola* is a comparatively inactive, sedentary species that usually exposes its anterior end only above the substratum. Approach of predators would be signalled by touch, vibration of the ground, water currents, and passing shadows, all stimuli to which the animal is sensitive in varying degree and to which it responds by a single contraction that jerks it back into its tube. Weak or subthreshold stimuli, at short enough interval to cause summation, would also cause its withdrawal, and strong repeated stimuli would result in successive quick contractions and further shortening. Since the animal elongates again rather slowly after a giant fiber response it would appear that short segmental neurones take over after each giant axon discharge and maintain the animal in a state of tonus from which it is only slowly released, thereby retarding exposure of the head and the crown for a considerable interval.

As far as is known, all sabellids and serpulids possess well-developed giant axons and exhibit quick reflex shortening similar to that observed in *Myxicola*. In *Sabella*, at least, the two giant fibers anastomose by transverse branches in each segment to form a composite giant axon and they probably function as a unit as in *Myxicola*. However, since the giant axons of polychaetes display the most diverse form and arrangement in species of different families, and even within a family, caution should be exercised in describing their function until more is known regarding the behavior of various representatives of this order. Other types of synergic contractions apart from symmetrical end-to-end shortening have been described in several polychaete species, and the possibility that giant axons may be involved in some of these contractions should not be discounted.

Acknowledgments

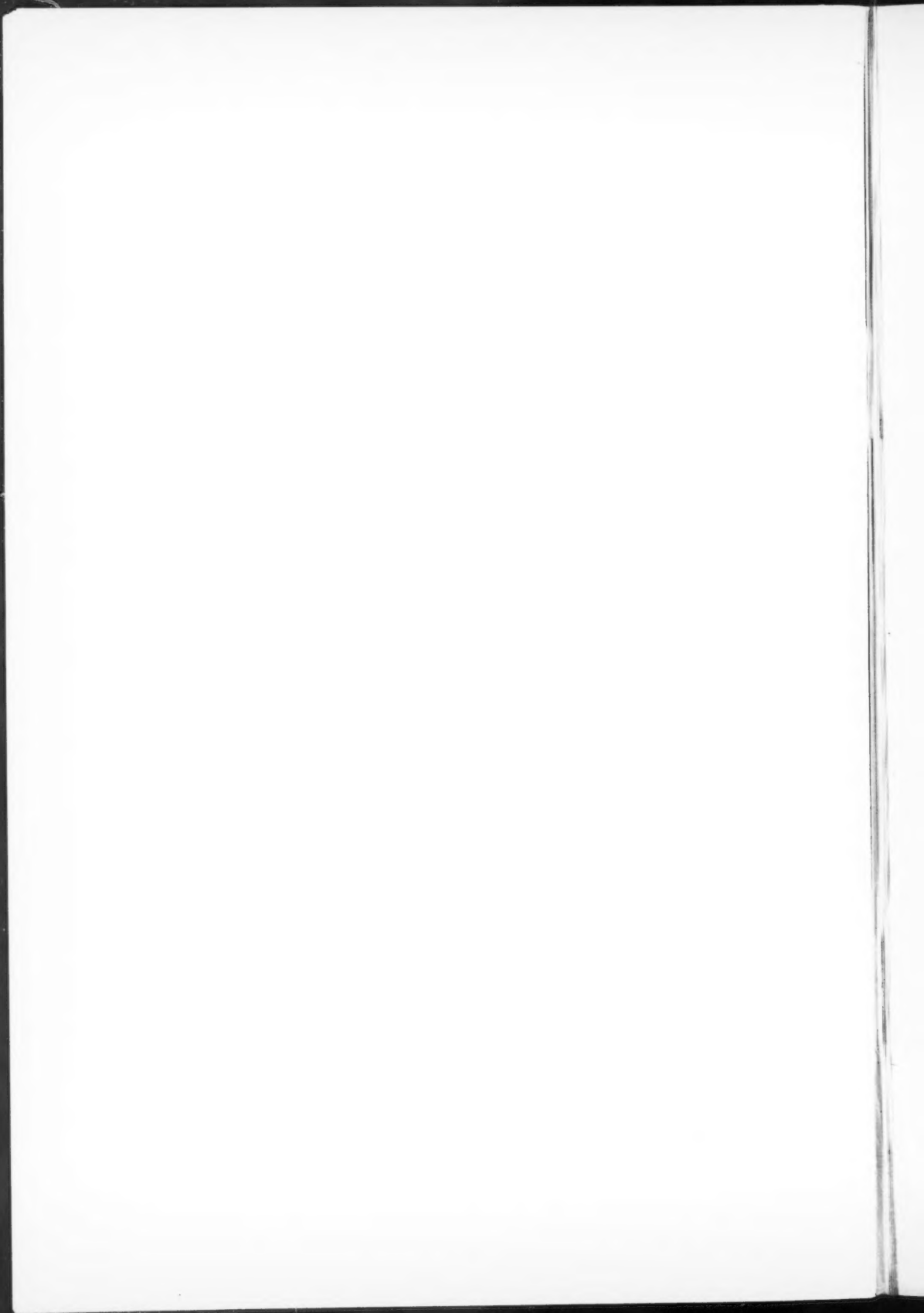
The writer is indebted to Prof. A. C. Hardy for facilities provided in the Department of Zoology and Comparative Anatomy, Oxford. Part of this work was done during tenure of the Oxford Table at Plymouth and it is a pleasure to acknowledge the co-operation extended by the Director and his staff at Plymouth. Sincere thanks are due to Mr. W. Russell of New College, Oxford, for assistance with the experiments. Prof. J. Z. Young has kindly offered suggestions. Financial assistance during the course of this study was obtained from the Department of Veterans' Affairs (Canada), the British Council, and the Carnegie Fund for Overseas Students.

References

1. BOVARD, J. F. The transmission of nervous impulses in relation to locomotion in the earthworm. Univ. Calif. Pub. Zool. 18 : 103-134. 1918.
2. BOVARD, J. F. The function of the giant fibers in earthworms. Univ. Calif. Pub. Zool. 18 : 135-144. 1918.
3. BUDDENBROCK, W. v. Grundriss der vergleichenden Physiologie. Gebrüder Borntraeger, Berlin. 1928.
4. BULLOCK, T. H. Functional organization of the giant fiber system of *Lumbricus*. J. Neurophysiol. 8 : 55-71. 1945.

5. BULLOCK, T. H. Organization of the giant nerve fiber system in *Neanthes virens*. Biol. Bull. 89 : 185-186. 1945.
6. CLAPARÈDE, E. Les annélides chétopodes du Golfe de Naples. Mém. soc. phys. Genève, 20 : 365-542. 1870.
7. CLAPARÈDE, E. Recherches sur la structure des annélides sédentaires. Mém. soc. phys. Genève, 22 : 1-200. 1873.
8. CUNNINGHAM, J. T. On some points in the anatomy of Polychaeta. Quart. J. Micr. Sci. 28 : 239-278. 1887.
9. ECCLES, J. C., GRANIT, R., and YOUNG, J. Z. Impulses in the giant nerve fibres of earthworms. J. Physiol. 77 : P23-P25. 1933.
10. FRIEDLÄNDER, B. Ueber das Kriechen der Regenwürmer. Biol. Zentr. 8 : 363-366. 1888.
11. FRIEDLÄNDER, B. Über die markhaltigen Nervenfasern und Neurochorde der Crustaceen und Anneliden. Mitt. Zool. Sta. Neapel, 9 : 205-265. 1889.
12. FRIEDLÄNDER, B. Beiträge zur Physiologie des Centralnervensystems und des Bewegungsmechanismus der Regenwürmer. Pflügers Arch. ges. Physiol. 58 : 168-206. 1894.
13. GRAY, J. Studies in animal locomotion. VIII. The kinetics of locomotion of *Nereis diversicolor*. J. Exptl. Biol. 16 : 9-17. 1939.
14. HALL, D. M. and PANTIN, C. F. A. The nerve net of the Actinozoa. V. Temperature and facilitation in *Metridium senile*. J. Exptl. Biol. 14 : 71-78. 1937.
15. HAMAKER, J. I. The nervous system of *Nereis virens* Sars. A study in comparative neurology. Bull. Museum Comp. Zool. Harvard, 32 : 87-124. 1898.
16. HARGITT, C. W. Observations on the behavior of tubicolous annelids. III. Biol. Bull. 22 : 67-94. 1912.
17. MONTAGU, G. Description of several marine animals found on the south coast of Devonshire. Trans. Linnean Soc. London, Zool. 9 : 81-114. 1808.
18. NICOL, J. A. C. The giant nerve fibres in the central nervous system of *Myxicola* (Polychaeta, Sabellidae). Quart. J. Micr. Sci. 89 : 1-45.
19. NICOL, J. A. C. and YOUNG, J. Z. Giant nerve fibre of *Myxicola infundibulum* (Grube). Nature, 158 : 167. 1946.
20. NICOL, J. A. C., SMYTH, C. N., and WHITTERIDGE, D. Conduction velocity in relation to axon diameter in *myxicola infundibulum*. Abstracts of Communications. XVII Intern. Physiol. Congr., Oxford. 1947.
21. PRUVOT, G. Recherches anatomiques et morphologiques sur le système nerveux des annélides polychètes. Arch. zool. exptl. gén. 3 : 211-336. 1885.
22. RUSHTON, W. A. H. Motor response from giant fibres in the earthworm. Nature, 156 : 109-110. 1945.
23. RUSHTON, W. A. H. Reflex conduction in the giant fibres of the earthworm. Proc. Roy. Soc. London, B, 133 : 109-120. 1946.
24. STOUGH, H. B. Giant nerve fibers of the earthworm. J. Comp. Neurol. 109-463. 1926.
25. STOUGH, H. B. Polarization of the giant nerve fibers of the earthworm. J. Comp. Neurol. 50 : 217-230. 1930.
26. TEN CATE, J. Sur la fonction des neurochordes de la chaîne ventrale du ver de terre (*Lambricus terrestris*). Arch. néerl. physiol. 23 : 136-140. 1938.
27. YOLTON, L. W. The effects of cutting the giant fibers in the earthworm, *Eisenia foetida* (Sav.). Proc. Nat. Acad. Sci. 9 : 383-385. 1923.





CANADIAN JOURNAL OF RESEARCH

Notes on the Preparation of Copy

GENERAL:—Manuscripts should be typewritten, double spaced, and the **original and one extra copy** submitted. Style, arrangement, spelling, and abbreviations should conform to the usage of this Journal. Names of all simple compounds, rather than their formulae, should be used in the text. Greek letters or unusual signs should be written plainly or explained by marginal notes. Superscripts and subscripts must be legible and carefully placed. Manuscripts should be carefully checked before being submitted, to reduce the need for changes after the type has been set. If authors require changes to be made after the type is set, they will be charged for changes that are considered to be excessive. **All pages, whether text, figures, or tables, should be numbered.**

ABSTRACT:—An abstract of not more than about 200 words, indicating the scope of the work and the principal findings, is required.

ILLUSTRATIONS:

(i) **Line Drawings:**—All lines should be of sufficient thickness to reproduce well. Drawings should be carefully made with India ink on white drawing paper, blue tracing linen, or co-ordinate paper **ruled in blue only**; any co-ordinate lines that are to appear in the reproduction should be ruled in black ink. Paper ruled in **green, yellow, or red should not be used** unless it is desired to have all the co-ordinate lines show. Lettering and numerals should be neatly done in India ink preferably with a stencil (**do not use typewriting**) and be of such size that they will be legible and not less than one millimetre in height when reproduced in a cut three inches wide. All experimental points should be carefully drawn with instruments. Illustrations need not be more than two or three times the size of the desired reproduction, but the ratio of height to width should conform with that of the type page. **The original drawings and one set of small but clear photographic copies are to be submitted.**

(ii) **Photographs:**—Prints should be made on glossy paper, with strong contrasts; they should be trimmed to remove all extraneous material so that essential features only are shown. Photographs should be submitted **in duplicate**; if they are to be reproduced in groups, one set should be so arranged and mounted on cardboard with rubber cement; the duplicate set should be unmounted.

(iii) **General:**—**The author's name, title of paper, and figure number should be written in the lower left hand corner (outside the illustration proper) of the sheets on which the illustrations appear.** Captions should not be written on the illustrations, but typed on a separate page of the manuscript. All figures (including each figure of the plates) should be numbered consecutively from 1 up (arabic numerals). **Each figure should be referred to in the text.** If authors desire to alter a cut, they will be charged for the new cut.

TABLES:—Titles should be given for all tables, which should be numbered in Roman numerals. Column heads should be brief and textual matter in tables confined to a minimum. **Each table should be referred to in the text.**

REFERENCES:—These should be listed **alphabetically by authors' names, numbered in that order, and placed at the end of the paper.** The form of literature citation should be that used in the respective sections of this Journal. **Titles of papers should not be given in references listed in Sections A, B, E, and F, but must be given in references listed in Sections C and D.** The first page only of the references cited in papers appearing in Sections A, B, and E should be given. **All citations should be checked with the original articles.** Each citation should be referred to in the text by means of the key number; in Sections C and D the author's name and the date of publication may be included with the key number if desired.

The *Canadian Journal of Research* conforms in general with the practice outlined in the *Canadian Government Editorial Style Manual*, published by the Department of Public Printing and Stationery, Ottawa.

Reprints

Fifty reprints of each paper without covers are supplied free. Additional reprints, if required, will be supplied according to a prescribed schedule of charges. On request, covers can be furnished at cost.



